

REPRODUCTIVE BIOLOGY OF THE TREE
IPOMOEA WOLCOTTIANA (CONVOLVULACEAE)

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ABSTRACT

Ipomoea wolcottiana is an hermaphroditic tree of the tropical deciduous forest of México. It flowers after leaf drop, but may be highly asynchronous among trees if interrupted by rainfall early in the dry season. Anthesis is nocturnal and nectar secretion is constant until after midday. Insect visitors include sphingid moths and 21 species of bees; few of these have characteristics of effective cross-pollinators. The fragrant flowers present abundant pollen, but the sucrose-rich nectar differs between trees by as much as a factor of three. Significant individual variation also occurs in stamen and style length, and flower weight, but only the latter two are correlated. Pollination experiments show self-incompatibility and some female-sterile trees; the latter result is supported by records of up to four years from marked trees, and is unrelated to floral morphology or nectar volume.

Variation between individuals in female fecundity is conspicuous in some species of *Ipomoea*, but the causes have proven difficult to unravel (Martin 1970, Stucky and Beckmann 1982). Although *Ipomoea* is principally a genus of vines, a few species are trees (Lujan 1974, McPherson 1982), a life form that differs substantially from vines in the pattern of breeding systems (Bullock 1985). Tree species of *Ipomoea* are of broader ecological interest because they are common pioneers in the seasonally arid tropics of México, and may have an important role in supporting bee populations in a season when few other trees are in flower ("keystone mutualists" of Gilbert 1980). In this study, we outline the reproductive biology of *I. wolcottiana* Rose, including phenology, nectar production and quality, flower visitors, morphological variation in the flowers, compatibility, and sterility.

STUDY AREA

The present study was carried out from 1980–1987 in lowland Jalisco, México, at the Estación de Biología Chamela (19°30'N,

105°03'W). The summer rainy season lasts about four months, but rains between November and early February account for 11% of the average annual precipitation, with a range of 0–30%; no measurable rain has been recorded from March through late May (Bullock 1986). The vegetation is tropical deciduous forest (Rzedowski 1978, Lott et al. 1987). The flora of the field station includes 20 species of *Ipomoea* (Lott 1985). *Ipomoea wolcottiana* is here a tree of 2–9 m or more, and is scarce except in large areas of disturbance.

MATERIALS AND METHODS

Measurements were made of 10 flowers from each of 17 trees, including length of the style (from the base of the free filament), and of the longest and shortest stamen filaments, and flower weight. Nectar volume was measured on various dates from flowers on 16 trees, with five flowers sampled per tree per hour (at 2330, 0300, 0600, 0900, and 1330 hr local time), although not all trees were collected at all hours. Nectar analyses were made for six trees and included methods described previously for sugars and amino acids (Baker and Baker 1975, Baker and Baker 1982), as well as screening for alkaloids (Dragendorff test), proteins (brom-phenol blue test), and phenolics (p-nitro aniline test). Sugar concentration was measured from nectar spotted on filter paper.

Activity periods of bees were recorded for hourly periods on five days in February and March 1985. The species were rated for abundance and behavioral observations were made, which complemented collections and observations made yearly since 1980. Bee sizes were measured as the width of the scutum at the tegula, for five females of each species (males in three species, see below). Additional observations were made to detect visits by bats and moths, and birds were noted during the day.

Compatibility tests followed the protocol of Bullock (1985), with a total of 17 trees tested in 1982 and 1983. Fruit set was zero on some of these trees, so a sample was marked for yearly observation of fruiting (24 trees in 1982, 36 in 1983–1985). A qualitative rating system with four levels (0–3) was used to accommodate the range of variation of several orders of magnitude and the differences due to canopy size.

Statistical analyses were one-way ANOVA, Spearman rank correlations (r_s), least-square linear regression (r^2) and analysis of covariance (Killian 1981), the Student-Newman-Keuls procedure, and the Mann-Whitney test (Zar 1974). Significance was accepted at the 0.05 level. Plant and animal specimens were deposited in the station's museum or at the Instituto de Biología, U.N.A.M., in México City.

RESULTS

Phenology. The trees flowered in the early months of the dry season, and most were leafless then. In April 1980, the population contained trees with only flowers or fruits, and a few individuals with both. This late and asynchronous reproduction may have been due to rain in late January and early February (46 mm). In 1981, following mid-January precipitation (124 mm), a similar phenology was noted. With no rain from November 1981 through May 1982, flowering occurred in January and February 1982. Leaf fall was well advanced in November 1982, but heavy rains in late November and December (160 mm) caused a major leaf flush (sudden, vigorous growth). Flowering throughout the population was delayed until late February to early March 1983. The next dry season began in November 1983, and flowering followed in January and February, with rain in mid-January (38 mm) causing only a minor flush. The 1984–1985 dry season started in October, but rain in mid-December (85 mm) and in mid-January (19 mm) delayed flowering. In 1986, flowering was very sparse and fruit production zero, presumably due to lack of rain in summer 1985 (60% of previous normal). The next flowering season began in December 1986, and was not interrupted by mid-January rain (25 mm). Near the station buildings, well-watered trees retained some leaves year round, whereas unirrigated trees nearby lost all their leaves in the dry season.

Anthesis. The corolla was furled in bud, and opened gradually after midnight, until the distal half of the corolla was flared perpendicular to the floral axis. The entrance to the effective corolla tube was about 11–12 mm in diameter (Fig. 1). At anthesis, the anthers were dehisced and nectar was present. The flowers closed permanently the following afternoon.

Nectar. Nectar accumulated throughout the night and morning until at least 1300 hr. The volume-time regressions were all significant and ranged from $r^2 = 0.41$ – 0.94 . Rates of accumulation were heterogeneous (analysis of covariance, $F = 41$), varying from 0.90 – $1.98 \mu\text{l/hr}$. The estimated volume prior to anthesis (2300 hr) differed more than flow rates between trees, ranging from 0.6 – $16.2 \mu\text{l}$. Because the nectar accumulation curves were not heterogeneous in form, the trees can be compared most simply by the volume at a particular hour. At 0900 hr, somewhat after the peak of pollinator activity, accumulated volumes ranged from 11 – $34 \mu\text{l}$ (Table 1). The variation was nearly continuous, with no significant differences between trees differing in rank by less than three (SNK test). No significant trend emerged in relating flower weight to nectar volume ($r_s = 0.51$, Table 1). No significant correlations were found between nectar volume and length of style or stamen ($r_s = -0.09$, -0.10 , respectively). Furthermore, nectar production was not clearly related

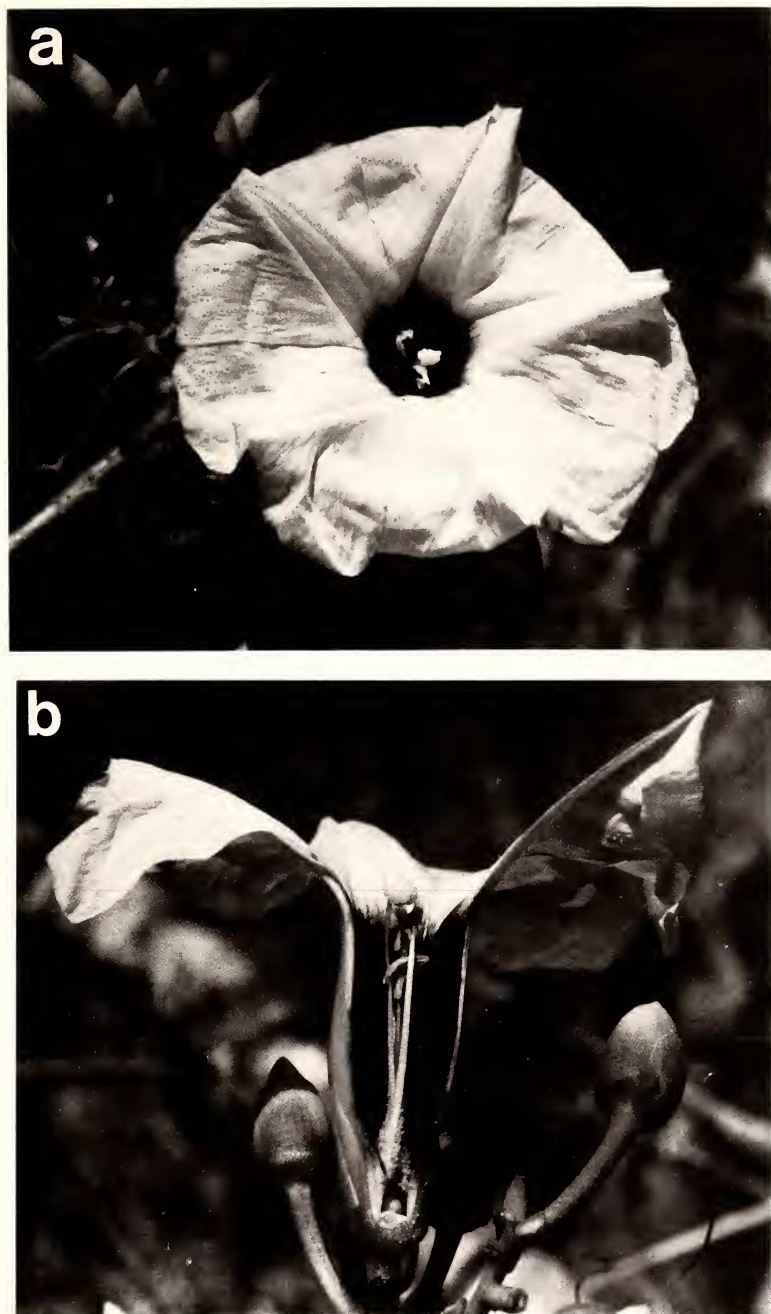


FIG. 1. Flower of *Ipomoea wolcottiana* in nearly axial (a) and cross-sectional (b) views (in situ, unfiltered daylight).

TABLE 1. FLORAL CHARACTERISTICS AND FRUIT SET FROM HAND POLLINATION IN *Ipomoea wolcottiana*. For morphology and nectar volume, the mean and standard deviation are given. Fruit set is given as the proportion (p) of the number of treated flowers (n).

Tree no.	Flower dry weight (mg)	Longest filament length (mm)	Style length (mm)	Nectar volume (μ l)	Fruit from hand pollination			
					Cross		Self	
					p	(n)	p	(n)
5	15.5 \pm 1.0	24.7 \pm 1.8	27.5 \pm 1.5	26.3 \pm 4.1	0.00	(9)	0.00	(17)
11	13.2 \pm 1.1	26.1 \pm 0.7	27.7 \pm 0.9	13.3 \pm 2.3	0.40	(10)	0.00	(17)
15	14.7 \pm 0.8	23.6 \pm 7.0	25.4 \pm 1.0	31.8 \pm 2.9	0.07	(15)	0.00	(17)
20	13.2 \pm 1.0	21.9 \pm 0.7	23.3 \pm 1.3	26.0 \pm 5.3	0.00	(6)	0.00	(12)
21	12.5 \pm 0.4	24.8 \pm 0.9	23.6 \pm 1.2	19.2 \pm 4.1	0.00	(11)	0.00	(11)
25	13.0 \pm 1.1	25.6 \pm 1.1	25.1 \pm 0.7	20.6 \pm 4.7	0.57	(14)	0.00	(19)
26	16.1 \pm 1.4	25.9 \pm 0.6	27.8 \pm 1.0	26.6 \pm 4.2	0.08	(26)	0.00	(25)
27	14.8 \pm 0.4	25.5 \pm 0.8	23.7 \pm 1.5	30.5 \pm 3.2	0.00	(16)	0.00	(17)
28	12.0 \pm 1.5	25.3 \pm 1.2	27.4 \pm 1.0	— — —	0.00	(20)	0.00	(20)
29	14.3 \pm 1.4	25.7 \pm 1.2	28.4 \pm 1.2	25.1 \pm 3.0	0.04	(23)	0.06	(32)
30	13.4 \pm 0.8	27.9 \pm 1.3	24.1 \pm 1.0	13.4 \pm 1.4	0.56	(18)	0.00	(21)
31	14.8 \pm 1.0	28.9 \pm 0.7	31.1 \pm 1.3	23.0 \pm 3.1	0.00	(20)	0.00	(26)
32	14.4 \pm 0.6	26.4 \pm 0.5	29.0 \pm 0.9	15.8 \pm 1.4	0.24	(29)	0.00	(27)
33	15.8 \pm 0.6	23.7 \pm 1.2	28.8 \pm 1.3	13.9 \pm 5.0	0.00	(39)	0.00	(30)
34	13.4 \pm 1.0	29.9 \pm 0.9	26.2 \pm 0.8	34.3 \pm 4.5	0.18	(22)	0.00	(34)
35	17.0 \pm 0.4	24.3 \pm 1.2	27.9 \pm 1.3	14.0 \pm 3.6	0.42	(19)	0.00	(40)
36	13.0 \pm 1.9	24.1 \pm 1.4	27.4 \pm 1.1	11.1 \pm 5.2	0.33	(24)	0.00	(23)

to fruit production from hand cross-pollination ($r_s = -0.20$). The volume in trees that are fertile by hand cross-pollination was not different from that of sterile trees (Mann-Whitney test).

Amino acid concentration in the nectar was low (1–2 on the histidine scale). The sugar component was mostly sucrose, with ratios of sucrose to glucose plus fructose ranging from 2.0–3.4 ($\bar{X} = 2.42$). Sugar concentration was measured for four trees, giving the following values: 25.8% (w/w), 29.6%, 27.7%, and 38.8%. None of the samples showed detectable traces of alkaloids or proteins, but the reaction for phenolics varied from not detectable to moderately strong. The flowers also had a strong fragrance. Apparently glandular hairs were present on the lower part of the filaments, but secretions have not been obtained in analyzable quantity.

Flower visitors. Twenty-one species of bees were found feeding at the flowers, but nine of these were rare (Table 2). Most of the species were represented by females or workers, but only males were noted for *Eulaema polychroma*, *Melissodes tepaneca*, and *Melitoma marginella*. The activity of the nocturnal *Megalopta* sp. remained poorly defined due to their reaction to light. *Ceratina capitosa* spent much time inactive inside the flowers, but this behavior may be limited to males. The range of body widths was almost an order of magnitude (Table 2) and included the largest and smallest bees in the Chamela fauna. The larger species always brushed against the anthers, and usually the stigma, on entering. All bee species foraged for nectar by entering the corolla tube. All species can become dusted by fallen pollen in the corolla tube, but only six species were noted as pollen collectors, including four of the common species (Table 2).

Other diurnal visitors included *Cacicus melanicterus* (Bonaparte) (Aves: Icteridae) and *Amazilia rutila* (DeLattre) (Aves: Trochilidae). Nocturnal observations showed some visitation by *Erinnyis* sp. (Lepidoptera: Sphingidae) and we have identified pollen collected from *E. ello* (L.) as *I. wolcottiana*. No visits by bats have been observed.

Style and stamen length. The length of the style and longest stamen varied significantly between trees (Table 1; ANOVA, $F = 39$ and 35 , respectively). The length of styles but not of stamens was correlated with flower weight (respectively, $r_s = 0.52$, $p < 0.05$; $r_s = -0.02$). Stamen and style lengths were not significantly correlated ($r_s = 0.28$), but showed similar ranges of variation, 8.0 and 7.8 mm, respectively. Mean length of the shortest stamen varied significantly ($F = 21$, range 16.5–24.8 mm) and correlated with length of the longest stamen ($r_s = 0.58$).

Compatibility and sterility. Of those trees that bore any fruit as a result of pollination by hand, all except one were self-incompatible (Table 1). Because all hand pollination was done between 0630 hr

TABLE 2. BEE VISITORS TO FLOWERS OF *Ipomoea wolcottiana*. Size is scutum width in mm for females, or males (*). Activity period is time of day by hour intervals (n.d. = species not observed in 1985). Notes are given for species observed collecting pollen (p), and for those more than rare in abundance.

Family and species	Size	Activity period and notes
HALICTIDAE		
<i>Augochlora smaragdina</i> Friese	1.9	9-13
<i>Augochlora albiceps</i> Friese	2.0	10-12 (p)
<i>Augochlora nigrocyanea</i> Cockerell	2.1	8-16 (p, few)
<i>Megalopta</i> sp	2.6	?0-7 (? , common)
ANTHOPHORIDAE		
<i>Ceratina capitosa</i> F. Sm.	2.4	8-17
<i>Ceratina</i> sp 1	1.2	10-17
<i>Ceratina</i> sp 2	1.0	10-14
<i>Centris nitida</i> F. Sm.	4.6	n.d.
<i>Centris segregata</i> Crawford	5.4	n.d.
<i>Melissodes tepaneca</i> Cresson	2.7*	9-15 (common)
<i>Melitoma marginella</i> (Cresson)	3.1*	8-15 (common)
<i>Xylocopa fimbriata</i> Fabricius	8.8	10-11
<i>Xylocopa mexicanorum</i> F. Sm.	6.9	6-12 (p, common)
<i>Xylocopa muscaria</i> (Fabricius)	5.2	11-12
<i>Xylocopa t. tabaniformis</i> (F. Sm.)	5.8	6-10 (p, common)
APIDAE		
<i>Eulaema polychroma</i> (Mocsary)	6.4*	10-11
<i>Melipona beecheii</i> Bennett	3.3	6-11 (few)
<i>Trigona buyssoni</i> Friese	0.9	9-13 (few)
<i>Trigona fulviventris</i> Guerin	1.6	8-12 (few)
<i>Trigona hellwegeri</i> Friese	1.8	n.d. (few)
<i>Trigona orizabaensis</i> Strand	1.7	6-17 (p, common)

and 1300 hr, there was no evidence for the breakdown of incompatibility barriers with flower age. No fruit were produced from hand pollination on seven of 17 trees tested, and 10 of 17 had fruit set of 10% or less. Fruit set was not significantly correlated with either style or stamen length or flower weight (Table 1; respectively, $r_s = 0.03, 0.31, \text{ and } -0.09$).

The exceptionally low fertility of *I. wolcottiana* compared with other tree species at Chamela (Bullock 1985) led to further observations in the population at large. Some trees of *I. wolcottiana* produced massive numbers of flowers, but produced few fruits or were completely barren, whereas adjacent trees, sometimes with interlaced canopies, produced many fruits. The differences between fruit production in trees with low and high fecundity were consistent. Data from four consecutive years showed no tendency to oscillate between barren and productive states, and the majority of trees of low or moderate average fecundity had no peak year (Table 3).

TABLE 3. MAXIMUM FRUIT PRODUCTION AND FREQUENCY OF (FRUIT-)BARREN YEARS FOR INDIVIDUALS OF *Ipomoea wolcottiana* WITH DIFFERENT AVERAGE FRUIT PRODUCTION.

Individual mean fruit production 1982 (or 83)– 1985	n	Percent of trees attaining a given maximum level of fruiting				Overall frequency (%) of tree-years with no fruit
		0	1	2	3	
0–0.49	8	88	12	0	0	97
0.50–1.39	8	—	62	38	0	10
1.40–2.19	7	—	—	57	43	0
2.20–3.0	13	—	—	—	100	4

DISCUSSION

The annual phenology of *I. wolcottiana* varies considerably and apparently is conditioned by the timing of rainfall. Thus, flowering may begin in early December or not until late February, or may split between early and late starting trees, and some individuals may flower twice in one season. Drought appears necessary for the onset of flowering, but rains in December or January can cause flushing in trees not well advanced in flower development. Desynchronized or delayed flowering has occurred in four years from 1980–1987. On a local spatial scale, soil and vegetation conditions affect the timing of drought experienced by the trees, which probably increases asynchrony in the population. Whatever the result for plant fitness, asynchronous and delayed flowering may benefit flower visitors by prolonging the availability of nectar. Also, the prolonged presence of immature fruit may benefit pre-dispersal seed predators (Schlising 1980, Augspurger 1981), which include *Megacerus cubicus* (Motschulsky) (Bruchidae), and unidentified species of Curculionidae, Diptera, and Lepidoptera. Other trees flowering during the dry season at Chamela are largely unresponsive to rain in those months.

The population is not limited to pollination by either nocturnal or diurnal animals. Nectar flow continues from late night anthesis to midday wilting. Also, the sugar and amino acid analyses are consistent with those from many species pollinated by sphingid moths or large bees (Baker and Baker 1982). Despite the observed diversity of visitors, most of the bees do not reliably contact the anthers or stigma on account of body size or behavior. Altogether, they must remove considerable nectar. *Xylocopa mexicanorum* and *X. tabaniformis* are the only bee species that pollinate *I. wolcottiana* consistently, are common, and move frequently between trees. *Ceratina capitosa* also might be a significant pollinator, as are its congeners on flowers of other *Ipomoea* species. Moreover, the importance of

nocturnal visitors remains to be clarified, especially for Sphingidae and *Megalopta*. Bats were not observed visiting *I. wolcottiana*, and the nectar sugar composition is contradictory to the trend in species pollinated by microchiroptera (Baker and Baker 1982). However, abundant pollen of *Ipomoea* sp. was found in stomachs of the bats *Leptonycteris yerbabuenae* Martínez and Villa and *Glossophaga soricina* Pallas in Guerrero (Quiroz et al. 1986).

Nectar quantity differs among individuals, but we presently have no reason to interpret variation around the linear regressions of quantity on time as representing time-varying secretion rate. The latter has been shown for a few trees and was suggested as a mechanism to induce cross-pollination (Frankie and Haber 1983).

Variation within and between individuals in style and stamen length has been reported in few *Ipomoea* species (Wilson 1977, Ennos 1981) despite many studies of pollination. In *I. wolcottiana*, the difference between longest and shortest stamens is always substantial (3–8.2 mm), although its distribution was not normal or unimodal. Greater anther-stigma distance entailed an order of magnitude greater outcrossing frequency in *I. purpurea* compared with *I. hederacea* (Ennos 1981). Also, seed set from autogamy in *I. purpurea* was negatively correlated with anther-stigma distance (Ennos 1981). The style-filament difference in *I. wolcottiana* ranged from –3.8 to 5.1 mm, but was not normal or unimodal, and was not different between trees that were fertile or barren in hand cross-pollination (Mann-Whitney test).

Thus, *Ipomoea wolcottiana* varies significantly in morphological and functional characters that are not sorted into well-defined groups or correlated in interpretable patterns. If the system is evolving, the path is unclear as yet. As a further element in the breeding system, variation in male fertility has not yet been detected. A limited search for male sterility, using cotton blue in lactophenol (in vitro germination of *Ipomoea* pollen is problematic; Martin and Ortiz 1966, Stucky and Beckmann 1982), did not show any notable differences among trees. A similar condition was described for *Mirabilis froebelii* (Behr) Greene (Nyctaginaceae; Baker 1964), where variability in the floral organs had no apparent relationship to the breeding system.

In fruit production, most variation was among trees of intermediate to low average fecundity, and non-fruiting trees were consistently barren. Thus, this *I. wolcottiana* population does not consist of individuals that fruit heavily on a supra-annual basis with intervening years of little or no fruit (Janzen 1978). The proportion of trees with different bearing levels is unknown, because the sample population was not taken at random. Barrenness might be due to nutrient limitation, lack of pollination, lack of compatible pollen, genetic sterility, or cytogenetic problems. The former two alternatives are not probable because trees with different levels of fecundity

(by natural or hand pollination) were frequently commingled. The consistent fruiting behavior or barrenness and the failure of pollination by hand to overcome barrenness of some trees lead us to conclude that some form(s) of female sterility exists in this population. As noted above, this is not correlated with a suite of floral characters. Female sterility is known in other *Ipomoea* species (Martin and Cabanillas 1966, Stucky and Beckmann 1982). Chromosomal aberrations and imbalance add to the problems in *I. batatas* (L.) Lam. (Ting et al. 1957). Thus, the sterility problem may require cytological study.

Female fecundity of some vine species is limited by the scarcity of compatible mates (Martin 1968, Stucky and Beckmann 1982). The potential for incompatible pollination is suggested by the results of extensive tests with the diploid *I. setifera* Poir., which revealed 10 incompatibility groups (Martin 1968). In vines, extensive clonal growth (Peñalosa 1984) or establishment from vegetative fragments may result in patches containing one or very few incompatibility groups. When plants establish only from seed, as in *I. wolcottiana*, lack of compatible mates seems unlikely to account for a wide range of fecundities. However, when trees are partially or completely self-incompatible, such a situation may arise. For example, in some sparse populations of *Inga* species (Mimosoideae) fruit set was limited by the low frequency of more distant and more successful crosses (Koptur 1984). The effects of population structure and its variation in the disturbance-following *I. wolcottiana* remain to be assessed in relation to both the generalized and individually variable characters of the breeding system we have described.

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